THE BIOLOGICAL SIGNIFICANCE OF EXOSKELETAL STRUCTURES IN THE PALAEOZOIC BRACHIOPOD GENUS *CHONETES*

by Edmund D. Gill, B.A., B.D.

Abstract

An attempt is made to interpret the functions of the various exoskeletal structures in *Chonetes* by a study of their form, their relationship to other structures, and their homologues in extant brachiopods. Attention has been paid especially to the spines on the ventral valve which are characteristic of the genus. Something of their ecology is inferred from their fossil occurrence. Finally, an attempt is made to estimate the phylogenetic significance of the facts and interpretations in this study.

Contents

Biological Significance of External Structures

1.—Structure of the Spines

The spines arranged along the cardinal margin of the ventral valve are the most distinctive feature of *Chonetes*. The spines are made of the same calcic material as the shell, and are hollow, as is seen when sections are cut and occasionally in decorticated specimens. The hollowness of the spines made them light yet strong. The cavity of the spine can be traced into the shell material, but no evidence has been found in the specimens studied to prove that the spine cavity connected with the cavity between the shells. However, for the spines to grow, there would need to be some membrane which could secrete the spine, and this would have to be connected with the animal between the valves. Perhaps this membrane atrophied when the spine was grown, and the aperture leading to the spine was closed.

The endopunctae of extant brachiopods may be regarded as homologues of the spines in the Chonetidae and Productidae. The mantle extends into these endopunctae, as no doubt it extended into the spines. The same material was secreted in the spine as in the main part of the shell, and so probably the same kind of cells did this work.

In chonetids the spines are usually straight whereas in productids they are more often curved. As a rule chonetid spines are inserted into the shell in the same direction as that in which they point. The chief exception is the genus *Longispina*, which, however, is very limited in number of species. Dunbar and Condra (1932) have shown an exception in *Chonetes granulifer* Owen (p. 139).

The angle at which the spines are set should be measured against the hinge-line, which is always straight, and not against the cardinal margin, which sometimes forms a vertex. The angle of insertion of the spines is genetically controlled, because it is the same for all members of the species, and it can be traced in lineages.

There was apparently a fairly active evolution in the spines of chonetids, judging by the immense variety found in them. The following types have been noted :

Type of Spines	Example
Long, straight and thin	*C. ruddockensis*
Short, straight and thin	*C. cresswelli*
Short, straight and thick	*C. robusta*
Short and sinuous	*C. killarensis*
Conical	*C. australis*
Gently curved	*C. melbournensis*
Oblique to hinge-line	*C. striatella*
At right angles to hinge-line	*C. setigera*
Deflected sub-parallel to hinge-line	*Longispina emmetensis*

2.—FUNCTION OF THE SPINES

Any structure in an animal falls into one of the three following categories :

    a. Biologically disadvantageous

    b. Of no biological advantage or disadvantage

    c. Biologically advantageous.

Natural selection operates for the removal of the first category and for the retention of the third. A structure which is biologically ' neutral ' may persist for the reason that it is not operated upon by natural selection. Changing ecological conditions may cause a neutral structure to become biologically significant.

The spines of *Chonetes* must fall in one of the above three categories. Against the first two possibilities is the fact that the genus continued with its spines for a period of time of the order of 150,000,000 years, i.e. about twice the length of the Tertiary Era (calculated from tables in Holmes, 1937). Moreover, there was a tendency in that time to increased spinosity (see Gill 1945, Fig. 1). The highly spinose family Productidae arose from *Chonetes*. Both the Chonetidae and Productidae continued as forms prolific both in numbers of species and numbers of individuals until the Permian Period, which witnessed the decline of the Brachiopoda as a whole. These two families contain the most successful brachiopods of all geological history. Their spinosity appears to have had something to do with their success.

Reversion gave rise to the non-spinose chonetids of the genus *Anoplia*, but these forms soon died out—a fact which suggests the spines had biological value. Moreover, a good deal of physiological activity would have to be expended on the production of spines (especially in the highly spinose Productidae), and it is reasonable to assume that unless this activity were of some advantage to the animal, natural selection would sooner or later have removed it. The spines exhibit a number of remarkable specializations, which suggests that natural selection favoured spines, sifting out suitable mutations.

That some advantage accrued from the presence of spines is suggested also by the developments which took place in the superfamily concerned. In the Chonetidae there was commonly a single row of spines along the cardinal margin of the ventral valve which probably held it above the sea floor. In

the Productidae, spines were present over more or less all the surface of both valves. In the Richthofeniidae where there were no spines, a similar elevation above the sea floor was attained by the thickening of the ventral valve. This thickening attained such proportions as to give the brachiopod the appearance of a cyathophylloid coral.

It is easy to see how spines could be of considerable biological advantage. Such shellfish, if without means of attachment or elevation, rested on the sea floor. The water at the bottom tends to be muddy, less oxygenated, and carrying less micro-organisms for food. The activities of organisms like trilobites also caused the mud of the sea-floor to be stirred up. Descending sediments reach their highest concentration near the bottom. If the spines acted as stilts to keep the animal off the sea floor (as was probably the case in the productids) or affixed the animal to some substratum (as was probably the case with the chonetids), then there would be a very definite biological advantage, for better respiration and food supply would be assured.

There appear to be two possibilities as to how the spines of *Chonetes* functioned, viz. :

    a. That the spines were a means of entangling the organism in marine plants, crinoids, and such like.

    b. That the spines became actually attached to some substratum. The evidence relative to these two views is summarized below.

Entanglement Theory	Attachment Theory
1. No definite callus has been observed on *Chonetes* spines, such as might be expected if they were cemented to a substratum.	1. The spines are fine and embedded in the matrix, so it is very difficult to determine for certain whether any callus is present or not.
2. The spines preserved whole usually taper to a point.	2. The spines are usually broken off, and this may be explained as due to their having been fixed and then snapped off. The complete spines would then be ones which did not become cemented.
	3. In the beds in which *Chonetes* occurs in Victoria, there is no evidence of forms with which the spines could become entangled apart from crinoids and possibly algae.
	4. Even if shells did become so entangled by their spines, the movement of the water would soon shake them down.
	5. The pedicle was lost early, and so probably the spines would not be sufficiently grown to act as an organ of entanglement.
	6. Even in adult life many forms (e.g. *C. hillarensis*) had spines which would be useless for such entanglement.

The evidence outlined indicates that the spines of *Chonetes* had some biological significance, and that their function was probably to attach the organism where better respiration and nourishment could be obtained. The operation of this function is imagined to have been as follows. The larva was free-swimming like that of extant brachiopods ; only so can the distribution

of the genus be explained. The larva affixed itself to some substratum by its pedicle and proceeded to develop. Early in development the shell was secreted providing a certain amount of protection for the developing animal. As the valves developed, the pedicle gradually became obsolescent. The spines becoming affixed to the substratum, took over the function of the atrophying pedicle. The preserved shells of *Chonetes* show that no functional pedicle was present in the adult.

The adult *Chonetes* was obviously a sedentary animal. Therefore if members of the genus were attached to something above the floor of the ocean, then they must have become attached in the free-swimming larval stage, the spines superceding the failing pedicle. If the spines did not take over the function of the pedicle before it atrophied, then the shellfish would fall to the sea-floor and the spines would be of little or no use. Many brachiopods such as *Crania, Davidsonia, Heteralosia, Juresania, Leptalosia, Petrocrania, Streptorhynchus Strophalosiina* and *Thecidea* were attached by cementation to some substratum. The spines of *Chonetes* are a biological equivalent of the callus which in the above-named genera acted as a means of attachment. In this view, the spines are just an elongated and refined callus, fulfilling essentially the same function, i.e. attachment.   Or, to use another comparison, the spines are the biological equivalent of a pedicle, for the pedicle also fulfills the function of attachment. Spines cannot be adjusted as a pedicle can, but, on the other hand, there is no physiological maintenance. Perhaps the highest specialization of attachment in brachiopods is seen in *Etheridgina* from the Carboniferous of Scotland, whose spines gripped a crinoid stem, and then the ventral valve became cemented to it (Davies 1920, p. 31).

3.—MECHANICS OF SPINES

Chonetes is believed to have had a semi-floating existence, i.e. it was attached to a sub-stratum, not by rigid cementation as when a valve is fixed by callus, but by means of elongations of the exoskeleton (the spines) which allowed a certain amount of movement in water currents. The spines were closely adapted for such a habitat in that they were constructed to give strength with lightness. This was achieved by their pipe-like build.

Engineers make wide use of the fact that, relative to the weight of the material used, a hollow column has much greater strength than a solid pillar of the same diameter. Mr. H. H. Hinton, B.E.E., A.G.Inst. Tech., A.M.I.E. (Aust.), has kindly applied this principle to the study of the spines of *Chonetes*. Assuming that spines are made of homogeneous material which complies with Hooke's Law, formulae were derived taking into account the usual types of loading.* It was apparent that the spines in most cases would fracture under the influence of bending.

The equation quoted in the footnote brings up the problem of the material with which the spines were filled. In the active stages of growth, the spines

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*The relationship between the strength and the weight per unit length for hollow and solid spines subjected to bending is expressed by the following equation :

$$\frac{\text{Strength per unit weight, hollow}}{\text{Strength per unit weight, solid}} = \frac{(R_1{}^4 - R_2{}^4)\ (G_s - G_w)}{R\ R_1\ [(R_1{}^2 - R_2{}^2)\ G_h - R_2{}^2\ G_f - R_1{}^2\ G_w]}$$

where R = radius of solid spine
   R_1 = outside radius of hollow spine
   R_2 = inside radius of hollow spine
   G_f = weight per unit volume of material with which the hollow spine is filled.
   G_h = do. of material of which the hollow spine is made
   G_s = do. of material of which solid spine is made
   G_w = do. of water in which spine is located.

must have been lined with a layer of lime-secreting cells ; only so could the spines be formed. The centre may have been filled with parenchymatous tissue, or gas-filled. As no connection of the spine cavity with the mantle cavity in mature shells has been demonstrated in the species studied (although proved for the Pennsylvanian species *C. granulifer*—Dunbar and Condra, 1932, p. 139) it is possible that the membrane in the spine atrophied, and the orifice was closed off by the mantle secretions on the inside of the shell whereby the valves were thickened. Productid spines had their cavities sealed off in this way. As one is unable at present to prove what was the nature of the material filling the spine, it is suggested that its weight per unit volume be taken as the same as the water surrounding the outside of the spine for the purposes of the present calculation. On this assumption, the factor G_f can be eliminated from the equation. The relative strength weight for weight of a solid spine as against a hollow spine of the same diameter will now be considered, so R can be equated with R_1. Thus simplified, the equation will read

$$\frac{\text{Strength per unit weight, hollow}}{\text{Strength per unit weight, solid}} = 1 + \frac{R_2^2}{R^2}$$

Thus, if the external radius of a hollow spine is 1 mm. and the internal radius 0·5 mm., then the relative strengths of a hollow and solid spine weight for weight will be 1·25 : 1, i.e. under the conditions of immersion in water in which *Chonetes* lived, a certain amount of calcium carbonate expended in a hollow spine having a cavity diameter of half the outside diameter, would give 1·25 times the strength as when used to build a solid spine. If the external and internal diameters were 1 m.m and 0·9 mm. respectively, then the relative strengths of a hollow and solid spine weight for weight would be 1·8 : 1. This means a physiological advantage of strength with lightness and conservation of biochemical activity.

Another structural feature worthy of notice is the strengthening of the spine at a likely point of failure, viz., where it joins the valve. Strengthening is effected by thickening. The cavity of the spine is not changed in diameter, but the wall is thickened at the point of juncture of the spine with the valve (Fig. 1A).

In *Chonetes* the spines are set along the posterior margin of the ventral valve either at right angles or obliquely to the hingeline. The latter group strongly pre-dominates, and this fact is probably significant. If force is applied, for example, as shown in Fig. 1B, then the principle of leverage applies. A set of spines at right angles to the hingeline (as in Fig. 1B) would not be so effective in withstanding a force from the direction indicated as the same number of spines fixed obliquely (as in Fig. 1D). *Chonetes* could not so well withstand a force applied in a line vertical to the plane of the valves. Spines as those of *Productus* would then be more advantageous.

It has been noticed that when the spines in *Chonetes* are curved, they are invariably curved outwards.

4.—Shape of the Valves

The earliest symmetry, both palaeontologically and ontogenetically, is radial. This symmetry provides even contact between organism and environment ; it provides also even distances for the diffusion of physiological substances and transference of impulses. Specializations caused the radial symmetry to give way to a bilateral symmetry. In the Atremata and Neotremata, evidences of a primitive radial symmetry are apparent ; evidences are seen also in the ontogeny of extant brachiopods. In the Chonetidae, the bilateral symmetry is very strongly developed, the organism being characterized by inequi-
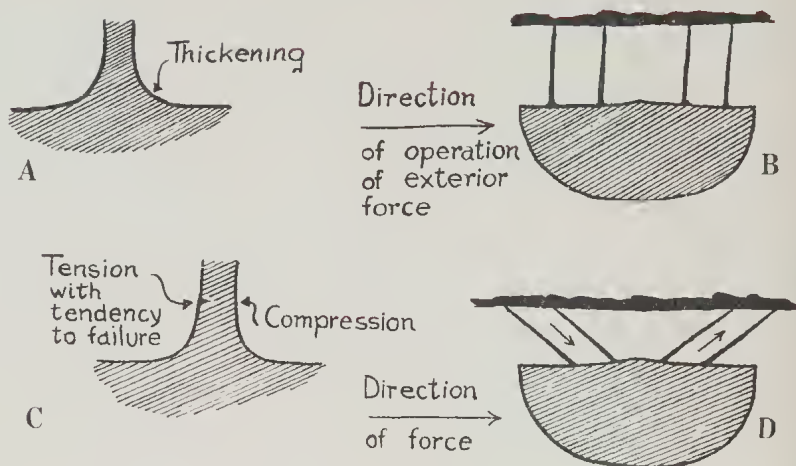
Fig. 1.   Mechanics of the Spines

A.   Strengthening of spine at insertion into shell by thickening.
B.   *Chonetes* attached to substratum. Lever effect when spines at right angles to hinge line.
C.   Nature of forces operating on spines in B.
D.   To show better distribution of forces through cross-section of spines when these are set at an angle to the hingeline.

valved equilateral shells, generally more or less semicircular in outline with a wide hingeline.

As in a number of brachiopods, the chonetids commonly have a median sinus in the ventral valve and a corresponding fold in the dorsal valve (e.g. *Chonetes cresswelli*). This condition is half-way to the full trilobation of the shell seen in genera like *Camarotoechia*. The biological values of the plication are probably :

a   To strengthen the shell ; compare the added rigidity gained by putting corrugations in corrugated iron.
b   The central channel in the shell would create a current of water in that direction. Judging by existing brachiopods the exhalant canal would be in the centre and this current would sweep away the animal's excreta. The configuration of the shell and the central current would also tend to create currents at the sides where the inhalant canals were probably situated. This would facilitate feeding and respiration (see Morse 1878, Lamont 1934).

A further interesting structural feature is the greater deposition of shell substance by the mantle in the umbonal area, i.e., where the forces imposed on the valves are greatest owing to muscle action, and to articulation. The shell thins off towards the anterior margin where such large forces do not operate. There is thus an economy of material and a combination of strength with lightness. This fits the semi-floating habit of *Chonetes* and contrasts with the heavy calcification of other strophomenoids like *Strophonelloides* and *Sulcatostrophia*. The thickness of the shell in the umbonal region indicates that the mantle of *Chonetes* must have secreted calcium carbonate not only at the edge but also on the inside of the shell. As the ventral protegulum grew outwards to form the adult valve, the umbonal region was progressively strengthened by further deposition of calcic material.

The umbo is negligible in *Chonetes*. The biological advantage of the umbo

appears to be to strengthen the shell and to protect the pedicle opening. With the need for lightness in *Chonetes* and the obsolescence of the pedicle, the umbo is negligible in size.

5.—ORNAMENT

From a biological point of view, there is no such thing in nature as 'ornament.' Every structure has a function, except where for a time a biologically neutral structure may escape the process of natural selection. The costae of *Chonetes* are an organ in the biological sense—a structure with a function. Morse (1902) has shown that costae are connected in extant brachiopods with setae. The setae are arranged around the anterior margin of the mantle, which rises over each seta, and so in secreting the exoskeleton forms a costa over each seta. In the extant brachiopods studied by Morse, each costa corresponds with a seta. If this applies to the Palaeozoic chonetids, then the costae are to be explained primarily as accommodations of the exoskeleton to irregularities of the mantle surface caused by the setae. The setae serve to exclude foreign bodies from between the valves, and the costae help to keep the setae in place. Lamont points out that where the environment is muddy, shells with fine ornament tend to occur, i.e. with setae set closely together and so able to cope with foreign bodies of small diameter. In the Victorian Chonetidae, there does not seem to be any correlation between the size of the costae and the type of enclosing sediments. If, as hypothecated, *Chonetes* lived attached to some substratum above the bottom, then correlation between size of costae and type of sediment would not be necessarily expected. However, the costae provide once again strength with lightness and minimum expenditure of constructive material on the same principle as the corrugating of iron sheets.

On the anterior margin, the costae involve the whole thickness of the shell. Sometimes this condition is maintained into maturity, i.e. no deposition of shell material takes place on the inside of the shell, and so all the ribs are reproduced on the inside of the shell over its whole area (e.g. *C. killarensis*). However, more often there is deposition by the mantle so that little of the ribbing appears on the interior of the shell. This is especially so in the area occupied by the muscle scars (e.g. *C. taggertyensis*). The wavy margins of costate valves ensures their close apposition upon closure.

Unless the costae increased in number towards the anterior margin, they would become increasingly separated. The increase is by bifurcation and/or by intercalation. The fact that the mode of increase generally holds for a species indicates that the structure was genetically controlled. The increase in number of costae no doubt represents an increase in the number of setae around the anterior margin, so that the spacing necessary for their effective action was maintained.

Biological Significance of Internal Structures

1.—MEDIAN SEPTUM

Although the valves of *Chonetes* needed to be light in view of its semi-floating mode of life, they needed also to be strong enough to withstand the action of the powerful adductor and diductor muscles, and to provide protection for the soft animal within. The median septum contributes to the achievement of these ends in the following ways :

a. It strengthens the valve in accordance with the buttress or T-iron principle—as commonly applied by engineers for providing strength with economy of materials and labour. Such a design keeps the exoskeleton of *Chonetes* light, gives the necessary strength, and avoids unnecessary physiological activity.

The median septum is a structure belonging essentially to the posterior end of the valve. Whether long (as in *C. taggertyensis*) or short (as in *C. killarensis*), it is always found in the umbonal region, i.e. where the greatest forces are exerted through muscle action and articulation. Variations from species to species are seen in the length, width, and height of the septum, and whether it terminates abruptly (as in *Anoplia australis*) or gradually merges into the floor of the shell (as in *Chonetes taggertyensis*). In spite of these variations the median septum is always highest and thickest in the umbonal region where strength is most needed.

A second biological advantage of the median septum is that

b. It provides increased area for muscle attachment, and new angles for muscle action. Support for this interpretation is found in the fact that the length of the septum in *Chonetes* is related to the size of the muscle scars (see Fig. 2A,B). Where there is a small muscle area there is a short septum, and
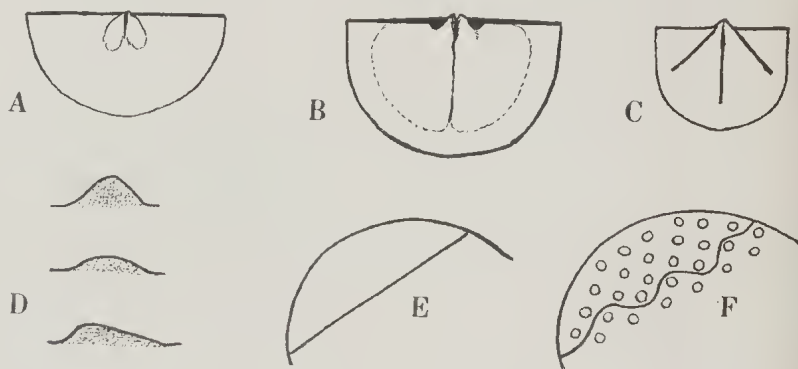

Fig. 2. INTERNAL STRUCTURES

A. Internal cast of ventral valve of a specimen of *Chonetes melbournensis* Chapman showing relationship of median septum to muscle scars.
B. Internal cast of ventral valve of a specimen of *Chonetes taggertyensis* Gill showing relationship of median septum to muscle scars.
C. Internal cast of ventral valve of a specimen of *Anoplia yeringae* showing accessory septa.
D. Types of papillae found in *Chonetes*. The upper two figures show the usual types, while the lowest illustrates the ' ramp ' type found in *Chonetes melbournensis* Chapman.
E. Straight fracture line which theoretically will occur in a flat piece of shell without papillae.
F. Lengthened fracture line when shell strengthened by papillae.

where there is a large muscle area there is a long median septum. It is known for certain that in some brachiopods the adductor muscles were attached to the median septum.

A further specialization is the anterior forking of the septum, a structure seen also in the closely related *Sowerbyella* (Jones 1928, p. 393) and in *Shaleria* (Caster 1939, p. 31). It has been recorded for *Chonetes* (e.g. *C. radiatulus* in Barrande 1879, Pl. 54, Fig. 1), and in *Anoplia* (e.g. *A. nucleata* in Schuchert and Maynard 1913, Pl. 13, Fig. 13). In Victoria this feature has been observed in a specimen of *Anoplia*, and in a *Chonetes* from Kinglake. The forked septum would further strengthen the shell, increase the area for muscle attachment, and the angles for the operation of the muscles.

The median septum is a structure very common in brachiopods, and of considerable taxonomic importance. For instance the presence or absence of

a septum distinguishes Brachyprionids from Douvillinoid Stropheodonts (Caster 1939, pp. 30-31).

2.—ACCESSORY SEPTA

Two accessory septa have been described for *Anoplia australis* and four for *A. withersi* (Gill, 1945). Septa additional to the median one are found also in quite a number of species of *Chonetes* (e.g. *C. coronatus* in Shimer and Shrock 1945, Pl. 134, Fig. 15). In most cases studied, the accessory septa do not actually reach the median septum (Fig. 2C). The septa are no doubt of similar biological value to the median septum. Plurality of septa is not uncommon among the Plectambonitids, which stresses again the close relationship between this family and the Chonetidae (cf. Gill 1945, pp. 128, 130-131).

3.—MUSCLE SCARS

The size, shape and degree of excavation of the muscle scars are characters of specific and sometimes generic importance. The scars of the Chonetidae are non-dendritic, and in this contrast with those of the Productidae. The size and disposition of the muscle scars in *Chonetes* suggest a strong and effective system. The central placing of the adductor muscles facilitates the closure of the valves. *C. taggertyensis* has a muscle field in the ventral valve which covers most of the interior of the shell, as it does in *C. sarcinulata* (Fig. 2B).

4.—PAPILLAE

Considerable variation is evident in the size and shape of papillae, but not so much in their distribution. Fig. 2D shows various types noted in the species recently described. In distribution, the papillae follow a regular pattern for each species, indicating that they are not incidental, like a pearl in an oyster shell, but genetically controlled. The heaviest concentration of papillae is on the cardinal angles and around the anterior margin. Where the costae appear on the interior surface, the papillae are usually set in the depressions of the internal surface, i.e., they do not jut out into the inter-valve cavity, but they stud (so strengthening) the costae of the external surface which, being the more prominent part of the surface, would be subject to greater and more frequent impulsive loading.

The wide distribution of papillae through genera and families of brachiopods, and their persistence through succeeding geological periods, suggests retention by natural selection of a structure of biological advantage. Morphologically, the papillae may be regarded as homologous with the external spines, i.e. they are short, rounded spines, interiorly directed.

A biological advantage of the papillae which can be proved for *Chonetes* is once again that of providing strength with lightness of weight and economy of physiological activity. Along the hinge-line and in the umbonal region the valves are strengthened by the shell being thicker and by the presence of a median and sometimes accessory septa. The shell is thinnest and so most liable to fracture at the cardinal angles and round the anterior margin. The papillae strengthen these areas where the exoskeleton is weakest and sudden forces may be imposed by collision, by the opening and shutting of the valves, etc. The added strength is proportional to the increase made necessary in the length of a fracture line round the papillae as against a direct line of fracture which would be possible where there were no papillae (Fig. 2E-F). The area of cross-section to be fractured is increased.

Sometimes (as in the dorsal interior of *C. melbournensis*) the papillae are found over the entire interior surface of a valve. In the muscle area, the papillae would give (like the median septum) greater area of attachment and a larger number of angles of pull.

5.—Articulating Apparatus

In all articulate shelly fossils, hinge structures are of primary classificatory importance. Biologically, these structures are of great moment too, because they are part of the complicated mechanism whereby the exoskeleton could be opened for active respiration and ingestion, but closed as a protective measure in time of danger. A gene complex controlled the deposition of calcium salts along the hinge-line so that instead of a solid layer being deposited as over the rest of the mantle, a series of structures were built which could be used for the articulation of the two valves, and for other functions.

The articulating apparatus in *Chonetes* consists of a hinge margin (with narrow palintrope) and ventral teeth of varying strength usually unsupported by dental lamellae, which accommodate between them the cardinal process of the dorsal valve. The long hinge margin provides a considerable articulating surface, and the teeth prevent any lateral movement such as takes place in some Inarticulata.

The hinge-line is specialized in *Eodevonaria* (Breger, 1906) by being crenulate. This structure appears to have arisen independently of the same feature in the Strophomenidae, i.e. they are homologues. *Eodevonaria* did not appear until Devonian times, and in its general form it so closely simulates Devonian species of *Chonetes* that one cannot doubt that it rose directly from them.

As far as the cardinal process is concerned, the Chonetidae are part of an evolutionary sequence which can be traced through the Strophomenaceae. In plectambonitids like *Leptellina*, the cardinal process is a simple ridge, while in other genera of the family, there is a simple cardinal process, sometimes grooved (*Sowerbyella*). In the Chonetidae the cardinal process is still a comparatively small structure, but its myophore becomes more specialized, being often quadrilobate (*Chonetes*). In the Strophomenidae the process is simple or pedunculate, commonly with a degree of specialization comparable with that in the Chonetidae. However, in the Productidae the cardinal process becomes relatively much larger and more specialized, and assumes considerable taxonomic importance. The process was a terminus for the attachment of the diductor muscle, and so the increased area and greater leverage (with greater length) would be a distinct advantage in the Productidae where the shells become larger and heavier than in the Chonetidae.

6.—Brachiophores

These are simple and nodular as a rule in *Chonetes*, no crura or brachidium being present. In the Chonetidae the brachiophores are very simple altogether, contrasting in a marked way with the elaborate cardinalia of some families of the Telotremata. However, the lophophore organization must have been fairly efficient, for the Chonetidae were one of the most prolific families in numbers, and one of the most enduring in time.

7.—Inter-valve Cavity

The various species of *Chonetes* are either concavo-convex (the more usual) or plano-convex, and the space between the valves small. If the shells are concavo-convex, then the two valves follow one another fairly closely. If they are plano-convex, then the convexity of the ventral valve is not very great. The small inter-valve cavity of *Chonetes* shows that the animal was a thin one and thus light—in keeping with the semi-floating existence it is believed to have had. I presume that the name *Chonetes* (from the Greek work for a funnel) was given the genus on account of the shallow inter-valve cavity. Sutton (1938) considers the size of the cavity important taxonomically.

Lamont claims that the small size of the inter-valve cavity and the fineness of the ornament would suggest adaptation to a muddy environment. Since *Chonetes* arose from mud-loving forms (see Gill, 1945), the presence of such adaptations are readily understood even if *Chonetes* was attached by its spines to a substratum. Furthermore, if the spines failed in their work of supporting the animal, then it would have to adapt itself to life on the sea floor.

The Ecology of Chonetes

The genus *Chonetes* is found in diverse facies. For example, it is found in the beds of Rhenish facies at Whittlesea, and beds of Bohemian facies at Lilydale. *Chonetes* has no terrestrial or pelagic species, as far as is known. The presence of *Chonetes* in a variety of facies makes it valuable as a stratigraphic index fossil. The success of *Chonetes* is no doubt linked with its adaptability to a number of environments.

Kulikov (1946) has recently studied the distribution of brachiopods in the Abdulino bioherm (Ural Mts.) as dependent on facies, and has noted that 'The brachiopods are strictly confined to definite facies of the reef massif. Only some few species belonging chiefly to *Productidae* were able to live in all the facies of the Abdulino reef.'

Dunbar and Condra (1932) write, 'Of all the families of brachiopods, the Chonetids are most useful for a general scheme of zonation, since they occur in abundance in nearly all fossiliferous horizons and display marked evolutional changes ' (p. 22).

Many species of *Chonetes* appear aggregated in great numbers, from which we may infer that they were ' gregarious ' in habit. Many extant brachiopods grow in great clusters.

Phylogenetic Implications

A survey of the very long history of the genus *Chonetes* shows that the same general form was maintained throughout ; there was much variation but no change in fundamental character. There must therefore have been a fairly stable gene complex present on the whole, allowing variation but avoiding the over-specialization which brought about the elimination of so many forms. The organism was well adapted, but at the same time successful in a variety of facies.

Addendum

Dr. Curt Teichert has kindly directed my attention to a paper by Schmidt (1938) who

1. Criticises Beecher's (1898) theory that spinosity is an expression of phylogerontism. This criticism holds as far as the Chonetidae are concerned, because that family was spinose throughout the whole of its exceedingly long palaeontological history.
2. Suggests that spines fulfilled a respiratory function. The great increase of surface provided by filiform extensions of a marine animal greatly aid respiration if they are in contact with the sea-water. But in *Chonetes* they were not. The mantle extensions in the spines were covered by a solid layer of calcareous material. Schmidt's theory is therefore unacceptable as far as *Chonetes* is concerned.
3. States that spinose forms are found in habitats with poor oxygen supply. This argument is not applicable to *Chonetes*, which is found in such a broad range of ecological conditions.

It is probable, in the writer's opinion, that no one explanation can be given for all spines. They are quite likely different organs in different animals ful-

filling quite different functions, although homoeomorphic.   All spines, in this view, are not homologues.

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